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Section 1

Spatio-temporal tuning of VEPs: effect of mode of stimulation

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Abstract

The spatial tuning function of the 8 Hz reversal Visual Evoked Potential (VEP) is frequently bimodal. This amplitude 'notch' largely disappears with 16 Hz pattern onset–offset (on–off) stimulation. To investigate the effect of temporal frequency on this phenomenon, we tested seven subjects using a range of rates centred on 8 Hz (reversal) and 16 Hz (on–off). With reversal, a deep notch was present at all temporal frequencies. A much shallower notch was evident with on–off. The on–off and reversal functions differed only in their low spatial frequency branches (below 4.5 c deg^{-1}) where, as temporal frequency decreased, the reversal response was reduced by 50%, whilst the on–off responses doubled in amplitude. Thus, although they behave differently with on–off and reversal, multiple spatial frequency mechanisms are evident with both forms of stimulation.

Keywords: Evoked potential; Amplitude; Spatio-temporal; Onset–offset; Contrast reversal

1. Introduction

There are numerous reports that the Visual Evoked Potential (VEP) corresponds to psychophysical observations. Although often reported as somewhat tenuous, this link has prompted workers to apply the technique in the objective evaluation of visual resolution and contrast sensitivity (Regan, 1977; Tyler et al., 1979; Norcia & Tyler, 1985; Allen et al., 1996). This approach is attractive as a means of evaluating visual function in neonates and infants. In such investigations, time is at a premium. It has therefore become common practice to use rapid presentation rates, in order to maximise the trade-off between information yield and recording time (Regan, 1972).

Rapid contrast reversal of a stimulus allows the spatial tuning characteristics of the VEP to be obtained in a relatively short time and for most spatial frequencies the relationship between contrast and amplitude is maintained. However it is apparent that using faster presentation rates leads to complex spatio-temporal interactions which influence the amplitude and phase of the signal. These complexities were starkly illustrated by Tyler et al. (1978); they showed that VEP amplitude was sharply tuned in the spatial domain and that the tuning depended on stimulus temporal frequency. Furthermore, they described (Fig. 10, p. 547) a range of spatial frequencies in which the link between VEP amplitude and contrast appeared to break down completely, leading to a severely attenuated response in the middle of the spatial frequency range investigated. Paradoxically, this 'notch' occurs with stimuli which are most visible (i.e. at the peak of the contrast sensitivity function). Strasburger et al. (1993) investigated this effect in some detail and confirmed that, with 8 Hz reversal presentation, a bimodal spatial frequency function is obtained in the majority of subjects. The effect all but disappears when 16 Hz on–off is used. They clearly showed that the spatial frequency notch occurs over a wide range of contrasts. It appears, then, that mode of stimulation influences when the amplitude–contrast relationship holds and when it breaks down.

An insight into how the dip in the spatial frequency function is formed is important. This may help to us to understand the way in which single unit electrical activity in the visual cortex is reflected in the form of slow wave signals at the scalp (Regan & Spekreijse, 1986).

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Furthermore, very little is known about the correspondence, if any, between signals recorded at the scalp and the coding of supra-threshold contrast. A detailed knowledge of the stimulus conditions which influence when amplitude is linked to contrast sensitivity (and when it is not) is essential in any VEP study of spatial vision. Finally, from a practical point of view, the spatial frequency notch limits the clinical value of VEP-based techniques. The conditions where the notch occurs (at least in adult studies) are precisely those which are critical for assessing visual function in infants.

In the present report we explore the effect of the mode of presentation on the spatial tuning of VEPs using a range of temporal frequencies, concentrating on the differences between on–off and contrast reversal stimulation. Whilst it is well-known that signals obtained with on–off presentation have different neural origins from the more commonly used contrast reversal (Spekreijse et al., 1973; Kulikowski, 1977; Kulikowski & Parry, 1987), there are few reports documenting the effect of the two forms of stimulus presentation, and fewer still which investigated a wide range of spatio-temporal frequencies. It is important to fill this gap in the literature. Many workers are faced with the choice between on–off and reversal and it is important to know how the mode of presentation, or any spatio-temporal interactions, will affect the results.

We have investigated the effect of temporal frequency and stimulus presentation mode on the VEP spatial tuning function for a wide range of spatio-temporal frequencies. We have concentrated on the amplitude of the steady-state response in the range 12–20 Hz. On–off and contrast reversal responses are compared across the range of spatial frequencies in which the reversal notch occurs, and where on–off presentation apparently eliminates it. The data reveal clear and unequivocal differences between the signals generated by the two forms of stimulation, particularly at low spatial frequencies.

2. Methods

2.1. Stimuli

Vertical sinusoidal gratings were generated on a high-resolution RGB graphics display (Barco CCID7651 'Calibrator'). The red, green and sync inputs of the monitor were driven by a Millipede Prisma VR1000 12-bit grating generator card in an IBM PC-compatible computer. This allowed the luminance of each of the vertical raster lines to be set between 0 and 80 cd m^{-2} in steps of 0.1 cd m^{-2}, correcting for the gamma characteristics of the monitor. In these studies, the red and green channels were used simultaneously to present gratings with the same mean luminance and spatial phase (thus producing a luminance-modulated yellow grating). The gratings were temporally modulated at a range of rates in either on–off (12, 13, 14, 15, 16, 17, 18 and 20 Hz) or pattern reversal (6, 6.5, 7, 7.5, 8, 8.5, 9 and 10 Hz) mode. For example, the 12 Hz on–off grating appeared for 41.7 ms, and was then replaced with a blank screen with the same mean hue and luminance for a further 41.7 ms. The 6 Hz reversal stimulus reversed in spatial phase every 83.3 ms. Six spatial frequencies were employed: 0.75, 1.5, 3.0, 4.5, 8.0 and 13.5 c deg^{-1}. On a raster-based display, the lowest spatial frequency is limited by screen size, and the highest by the resolution of the raster. All of the above spatial frequencies were viewed at the same distance (244 cm), and hence the coarsest pattern was composed of less than four complete cycles (3.75). Therefore some care should be taken in interpreting the data from this pattern. All gratings were spatially symmetrical. The screen was masked so that the gratings were presented in a circular field whose diameter was 5° when viewed at 244 cm. A small central fixation cross was provided. Mean luminance was 20 cd m^{-2}. Following Strasburger et al. (1993), who investigated a wide range of contrast, we employed a single contrast change of 0.4 for both forms of stimulation. Thus, for on–off, contrast changed from 0 to 0.4; for reversal, contrast changed from -0.2 to 0.2. The frame refresh rate of the monitor was adjusted (between 48 and 72 Hz) to allow each stimulus to change in synchrony with the frame synchronisation signal. In control experiments, we have established that such variation in frame rate does not affect the VEP (Hadjizenonos, 1996). The grating generator card could be programmed to supply, on software request, a TTL-compatible pulse of less than 100 μs duration in synchrony with the frame refresh signal. This provided the trigger for data acquisition.

2.2. VEP recording

EEG signals were acquired using a Medelec ER94a system, modified by the manufacturer to produce analogue output between $+0.5$ and -0.5V. Corner frequencies were set at 1 Hz (6 dB per octave) and 60 Hz (12 dB per octave). The analogue output was further amplified with a broad-band (DC-10 kHz) 10:1 amplifier and then fed into the analogue input of a CED1401 smart interface (Cambridge Electronic Design Ltd) which was controlled by the same computer as the stimulus. The CED1401 was used for storage and analysis of VEP waveforms. The VEP was derived from a 9 mm Ag/AgCl EEG electrode (SLE Ltd), attached to the occipital scalp at midline position Oz (10% of the inion–nasion distance above the inion). Differential input to the amplifier was derived from linked ear electrodes and a forehead electrode was connected to

ground. Electrode impedance was kept below 6 kΩ. Acquisition of each block of EEG samples was triggered by a TTL signal which occurred at the start of a video frame (see above). During calibration it was established that the amplifier characteristics did not influence phase in the temporal frequency range tested (12–20 Hz).

Binocular responses were recorded to all spatial frequencies and a single temporal frequency in one trial. The CED 1401 sampled the EEG at 256 Hz. Starting with the lowest spatial requency, ten 4 s samples, each triggered at frame refresh, were stored in memory and a running average computed. The averaged VEP was subjected to a Fourier transform in order to extract the amplitude and phase of the fundamental (F Hz, with on–off stimulation) or 2nd harmonic (2F Hz, with reversal) frequency. At low temporal frequencies, there was likely to be a significant contribution from higher harmonics. Indeed Norcia (personal communication) has pointed out that the added information gained from 4th, 6th and even 8th harmonics may, under some circumstances, be of value. However, in the present study, the contribution from higher harmonics was negligible when the analysed temporal frequency was greater than 12 Hz (i.e. with 6 Hz reversal or 12 Hz on–off). As a measure of noise, an adjacent frequency (F-1 or 2F-1) was also analysed. Phase was extracted from the Fourier transform and vector average and SD computed across subjects. For a description of this procedure, see chapter 2 of Mardia (1972). In a single recording session, all temporal frequencies were tested, starting with the lowest.

2.3. Contrast sensitivity

As with the VEP, binocular contrast sensitivity was measured to all spatial frequencies at one temporal frequency in a single trial. For each mode of presentation (on–off and reversal), each temporal frequency was tested in turn in a single session, starting with the lowest. Each contrast sensitivity function (CSF) was determined twice. For each spatial frequency, the subject viewed a blank screen with the same mean hue and luminance as the stimulus. Test gratings were presented for 4 s and reported as seen or unseen. Threshold was determined using a binary search technique in which the size of each subsequent contrast increment (if below threshold) or decrement (if above threshold) was halved. Thus the trial was concluded when the step was the smallest possible (0.002). By this means, threshold could be determined in a very small number of presentations (six plus the number of initial trials required to reach a super-threshold contrast; typically threshold is reached after 7–8 presentations). A CSF for the six spatial frequencies took about 4 min.

2.4. Subjects

Seven subjects (two female, five male), with a mean age of 27.4 (SD = 5.5) participated in the study. In all cases, their visual acuity was 6/5 in each eye, with appropriate correction.

3. Results

Fig. 1(a and b) illustrate the VEP amplitude and phase tuning functions and the corresponding contrast sensitivities for 16 Hz on–off and 8 Hz contrast reversal. These have been extracted from the data in order to clearly demonstrate the results of the Strasburger et al. (1993) study. Note that the VEP amplitude scales are different for the two modes of presentation. Because the peak reversal amplitude is some 55% of the on–off peak, the y-axis has in each case been linearly scaled to give the best fit to the contrast sensitivity data (Strasburger et al., 1993). The figures also show VEP noise levels.

As Kulikowski (1971) showed, the contrast sensitivity functions (CSF, shaded areas) are markedly different for the two forms of stimulation, particularly at low spatial frequencies. This low frequency attenuation is much less evident with contrast reversal than with on–off. At the lowest spatial frequency (0.75 c deg^{-1}), sensitivity is around 0.5 log units lower for on–off than for reversal. The shape of the on–off and reversal CSFs was independent of temporal frequency, and the data in Fig. 1 are therefore representative of all temporal frequencies. The attenuated contrast reversal VEP, obtained with the middle range of spatial frequencies, has

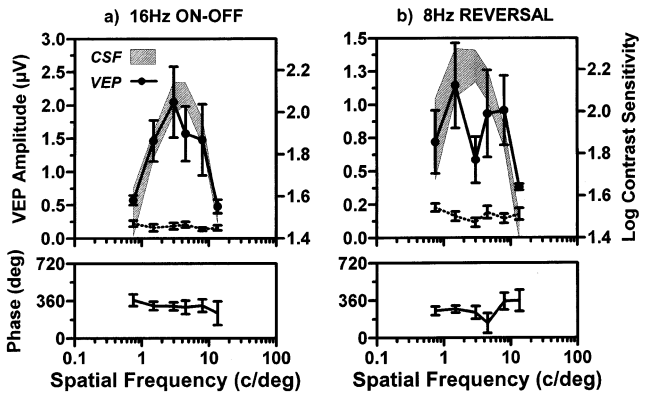

Fig. 1. Mean (±1 SE; $n = 7$) VEP amplitude (solid lines) and contrast sensitivity (shaded) as a function of spatial frequency, for (a) 16 Hz on–off and (b) 8 Hz reversal stimulation. Note that the amplitude axes in (a) and (b) are different, to obtain the best fit with the contrast sensitivity function. The dotted lines show amplitude of the VEP noise (15 Hz on–off and 7 Hz reversal). Phase (vector mean ± 1 SD) of the VEP is depicted in the lower graphs. Electrodes: Oz vs. linked ears. Mean luminance = 20 cd m^{-2}. Contrast change = 0.4. Field size = 5°.

also been well-documented. In our data, the low-amplitude zone occurs in the middle of the range for all subjects; as Strasburger et al. (1993) showed, this may not apply in all cases. They found that, in nine out of 19 subjects, the low-amplitude region was confined to low spatial frequencies, whereas in the others there was a notch in the tuning function, as in our data and as described in Tyler et al. (1978). In our 16 Hz data the notch is hardly evident when on–off stimulation is used. Overall, there is a higher signal:noise ratio and the VEP vs. spatial frequency function matches the shape of the corresponding contrast sensitivity function quite well, as Strasburger et al. (1993) showed. The phase data corresponding to the two forms of stimulation reflect the differences in the amplitude tuning functions. Phase is more variable with reversal, as would be expected when the signal to noise ratio is poor. In a parallel study, we have shown that on–off stimulation produces a simpler relationship between phase and temporal frequency than does reversal (Hadjizenonos et al., 1996).

The means of the VEP amplitudes for the same subjects as in Fig. 1 for the whole range of spatio-temporal frequencies are illustrated in Fig. 2(a and b). The data show that the marked differences between on–off and reversal responses, evident for the single temporal frequencies in Fig. 1, are emphasised when a range of temporal frequencies is employed. With reversal, the spatial frequency notch is unchanged throughout the temporal frequency range. With on–off, the slight discontinuity seen in Fig. 1(a) at 4.5 c deg^{-1} is present at every temporal frequency, and becomes more evident away from 16 Hz. Thus both on–off and reversal functions are divided into higher and lower spatial frequency branches. The shapes of the two functions are similar for the higher spatial frequencies, but at low spatial frequencies the differences are dramatic. Instead of being reduced in amplitude at the lower spatial frequencies, the on–off response shows a marked increase; this holds across the middle of the range tested and is reduced at the higher temporal frequencies.

As might be anticipated, and as seen in Fig. 3, the phase is variable for contrast reversal across all temporal frequencies. Fig. 1 shows, for 8 Hz reversal, that there is a phase change of about 200 deg between 4.5 and 8 c deg^{-1}, although the overall phase difference between the high and low spatial frequency ranges is more like 75 deg. This phase instability corresponds to the notch in the amplitude data. The on–off phase data are much more stable, displaying a small shift at the lower temporal frequencies. Interestingly, the on–off and reversal phase surfaces are most similar in the regions where their amplitudes differ most (i.e. at lower spatial frequencies).

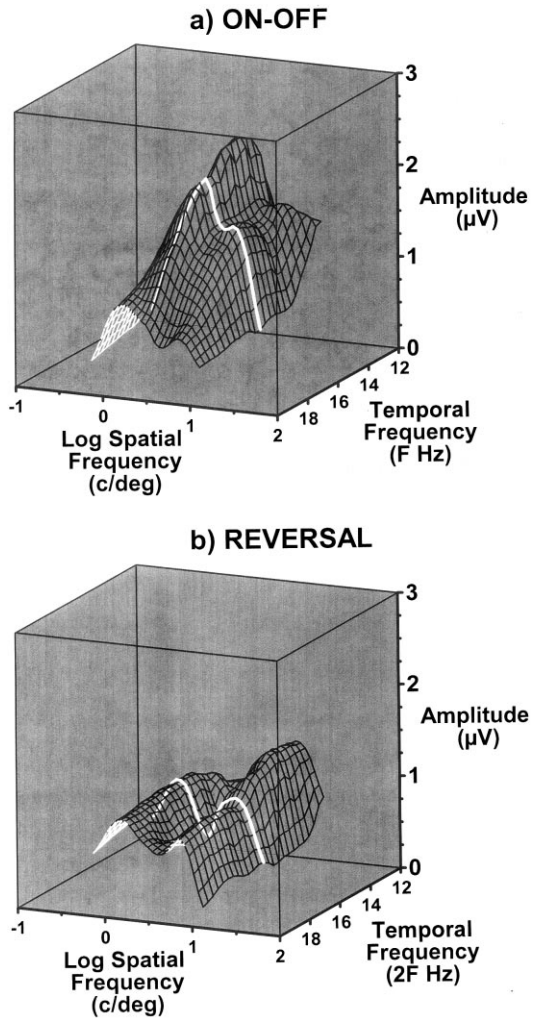

Fig. 2. Mean VEP amplitude as a function of spatial and temporal frequency for (a) on–off and (b) reversal presentation. The white lines mark the 16 Hz on–off and 8 Hz reversal data, and are the same as the VEP functions in Fig. 1. To aid interpretation of the figure, note that the highest temporal frequency (20 Hz) data are anchored to the front wall of the 3-dimensional plot. The fundamental frequency (F) is plotted for on–off (a) and the 2nd harmonic (2F) for reversal stimulation (b). Stimulus conditions as in Fig. 1.

From Fig. 2, it is evident that the main differences between on–off and reversal lie in the low spatial frequency region. To highlight this, we have replotted a low (1.5 c deg^{-1}; Fig. 4a) and a high (8.0 c deg^{-1}; Fig. 4b) spatial frequency as a function of temporal frequency. With 1.5 c deg^{-1}, as the analysed temporal frequency decreases below 16 Hz, on–off amplitude increases, and reversal amplitude decreases ($P < 0.05$; Wilcoxon signed rank test). Above 16 Hz, the functions are similar. With 8 c deg^{-1}, there is not such a marked difference between on–off and reversal. This interaction between mode of stimulation and spatio-temporal frequency is not seen at threshold in the contrast sensitivity data. We consider the VEP functions in more detail in the discussion.

4. Discussion

In a previous report, aimed at investigating the bimodal spatial tuning characteristics of the steady-state reversal VEP (Strasburger et al., 1993), it was demonstrated that if, instead of 8 Hz reversal, on–off stimulation at 16 Hz was used, then a single-peaked tuning function was obtained. The on–off stimulation was regarded as being the primary factor in generating a simple tuning curve. The main weakness in this argument was that, apart from 8 Hz, other stimulation rates were not examined. In the present report this issue has been addressed. The data show that, though the effect is much weaker than with reversal, on–off stimulation also produces a bimodal function at certain temporal frequencies. It may be that other studies which have reported a unimodal function have done so because of spatial frequency undersampling. Despite the presence of a notch in both on–off and reversal VEPs, there are fundamental differences in the spatio-temporal tuning characteristics of responses generated by the two forms of stimulation. The notch which occurs in the low to middle spatial frequency region is greater for reversal and, unlike with on–off, remains constant throughout the temporal frequency range. Furthermore, in the low spatial and temporal frequency range, the reversal response is severely attenuated whilst the on–off response increases.

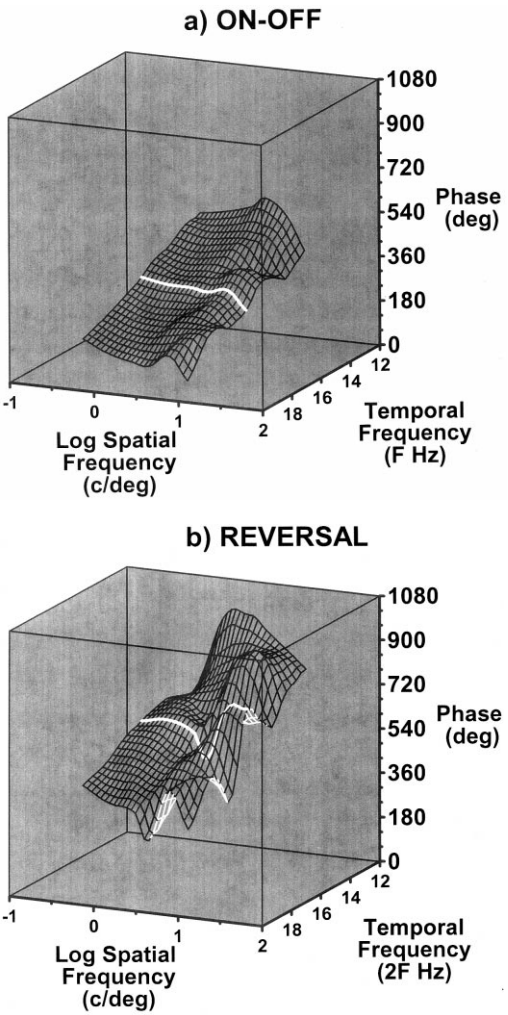

Fig. 3. The vector averaged phase equivalents of the VEP amplitude data in Fig. 2 for (a) on–off and (b) reversal presentation. Where necessary, multiples of 360° have been added to each data point to achieve the minimum phase difference across the surface. The white lines represent the 16 Hz on–off and 8 Hz reversal data. As in Fig. 2, the 20 Hz data are anchored to the front wall. For conditions, see Fig. 1.

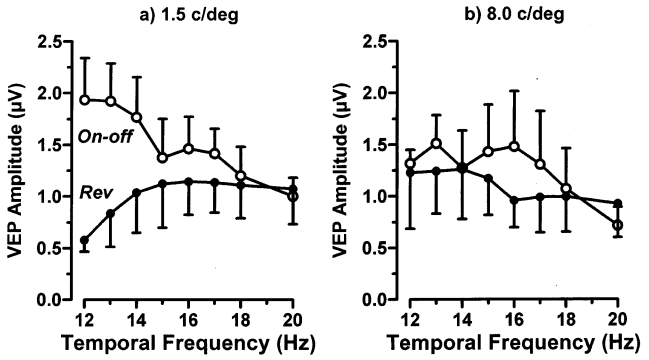

Fig. 4. VEP amplitude as a function of analysis rate for low (1.5 c deg^{-1}) and high (8.0 c deg^{-1}) spatial frequencies, to highlight the difference between on–off and reversal in the low spatial frequency branch. Data plotted are means ± 1 SE ($n = 7$). For conditions, see Fig. 1.

4.1. Multiple spatial mechanisms

It is commonly accepted that the processing of low and high spatial frequency information is mediated by different visual mechanisms (Keesey, 1972; Kulikowski & Tolhurst, 1973). VEPs reflect this, and the different properties of the VEP obtained from low and high spatial frequency stimuli have been extensively described. For example, Kulikowski (1977) employed slow presentation rates and distinguished 'transient' and 'sustained' type VEPs from low and high spatial frequencies respectively. Regan (1978) described the response from low frequencies as being dominated by 'local flicker' and that from higher spatial frequencies as 'pattern specific'. Low and high spatial frequency components of the VEP have also been identified on the basis of their differing contrast saturation characteristics (Spekreijse et al., 1973) and on their topographical scalp distribution (Regan, 1972). In the present study, data from a single, unipolar, electrode derivation are presented. In a study of scalp distribution and VEP spatial tuning, using a 2-dimensional Laplacean derivation, we have observed that differences between on–off and reversal responses cannot be simply attributed to scalp topography (Hadjizenonos, 1996).

The effects of at least two spatially tuned mechanisms are evident in the data in Fig. 2(a and b), in which a notch appears in the reversal data at 2–4 c deg^{-1}. In the same spatial frequency range there is a slight discontinuity in the on–off data, hinting that the same (or at least similar) underlying spatially tuned mechanisms are at work. Interestingly, this much weaker notch is less evident around 16 Hz than other temporal frequencies and this is the frequency (serendipitously) chosen in the Strasburger et al. (1993) study. It could be argued that the weakness of the notch in the on–off data may be an artefact of averaging. This would be so if the notch occurred at different spatial frequencies in different subjects. This was not the case in the present study. In both on–off and contrast reversal the attenuation of the VEP occurred in virtually the same region of spatial frequency for all subjects. With 16 Hz on–off presentation (i.e. the condition that gives the weakest notch), five out of the seven subjects had a reduction in amplitude at 4.5 c deg^{-1}. The other two subjects' amplitude vs. spatial frequency functions are monotonic at this temporal frequency, but produce a clear spatial frequency notch, again around 4.5 c deg^{-1}, at other temporal frequencies. With reversal, the functions were much less variable with temporal frequency, as the shape of the 3-dimensional surface in Fig. 2(b) reveals. Evidently, the observation of a weaker notch with on–off than with reversal is robust. We can conclude that there is clear evidence for the operation of at least two spatially tuned mechanisms in our data.

4.2. Spatio-temporal interactions

Psychophysical studies show that low temporal frequencies emphasize sensitivity to high spatial frequencies and high temporal frequencies emphasize sensitivity to low frequencies (Robson, 1966; Anderson & Burr, 1985; Watson, 1986). This interdependence between spatial and temporal properties of a stimulus has been demonstrated in VEPs. Regan (1978) showed how the spatial selectivity of contrast reversing VEPs depends on temporal frequency for both checks and gratings. VEPs to high spatial frequencies are largest at low temporal frequencies and vice versa. One of the objectives of the present study was to investigate the possibility that these spatio-temporal interactions may in some way account for the bimodal spatial tuning function of the contrast reversal VEP.

Regan (1978) observed that contrast reversal confounds spatial and temporal selectivity whilst on–off allows 'pattern' and 'local luminance' effects to be discriminated. This relates to low temporal rates (below about 3 Hz) where on and off responses are separated in time. The offset response, like reversal, encodes information about the change in contrast and thus can be said to be dominated by transient processes (Estevez & Spekreijse, 1974; Kulikowski, 1977). Onset responses, on the other hand, contain both transient and sustained components; differences between the two responses betray the operation of a sustained mechanism (Kulikowski & Parry, 1987). It is worth noting that, at these low presentation rates, there is no mid-spatial frequency amplitude notch (Plant et al., 1983; Vassilev et al., 1983; Russell et al., 1987).

Evidently, temporal frequency is an important factor. In order to establish the relative importance of mode of stimulation and presentation rate in the formation of the notch we have investigated the VEP over a range of spatio-temporal frequencies which 'bracketed' the conditions employed by Strasburger et al. (1993), namely 12–20 Hz and 0.75–13.5 c deg^{-1}. The following observations suggest that the mode of presentation is the more important factor.

First, the phase of the contrast reversal VEP is more variable and unstable as a function of spatial frequency than with on–off (Fig. 3a and b). We have also observed this in a study which specifically addresses the variation of phase with temporal frequency (Hadjizenonos et al., 1996). In the present study, phase values on either side of the notch were dramatically different (see Fig. 1). The phase differences observed could easily account for destructive interference of the signal. The on–off VEP is quite stable by comparison and would therefore be expected to generate a much larger signal by virtue of additive interactions.

The second point relates to the temporal tuning of the two types of response at low spatial frequencies. In Fig. 4a it is apparent that, whereas the on–off 1.5 c deg^{-1} VEP generally increases as temporal frequency decreases, the contrast reversal response undergoes a marked decrease. Finally, the temporal tuning of the higher spatial frequencies further emphasises the fact that the two modes of stimulation tap the underlying temporal mechanisms in different ways (Fig. 4b). Here we see the on–off response peaking when the contrast reversal response reaches a minimum (at 16 Hz). Interestingly, the high spatial frequency reversal and low spatial frequency on–off curves are similar, with dips at about the same analysed temporal frequency.

With the exception of the 1.5 c deg^{-1} reversal data, Fig. 4 shows discontinuities in the temporal tuning function which reflect Regan (1978) and are consistent with the operation of low and mid temporal frequency mechanisms. It should be noted that the temporal frequency range in our study is quite narrow compared with Regan's, and that his notch occurred at a lower temporal frequency (for 8 c deg^{-1} reversal it was at 11 Hz, whereas in the present study it is at 16 Hz). The relative predominance of the two temporally tuned mechanisms (and thus the position of a temporal notch) is likely to be strongly influenced by factors such as

temporal frequency, mode of stimulation and contrast (the latter unspecified in the Regan study).

Whatever the origins of the spatial notch, this study has practical implications for those interested in optimising the VEP signal to noise ratio. This is particularly important in studies of infant vision, when there is limited time available. In studies of spatial vision away from the resolution limit, the presence of a notch is undesirable. Although the temporal immaturity of the infant visual system means that the notch is rarely encountered in the first few months of life, it does become evident as the visual system matures. However, even where the aim is to estimate resolution limit (and in infant studies this is the most common use of the steady-state VEP), it is still beneficial to employ a stimulus which generates as strong a signal as possible. Adult and infant VEP studies in our own laboratories consistently yield better and more reliable results with on–off than with reversal (Parry & Murray, 1996; Strasburger et al., 1996). This study presents compelling evidence for the superiority of on–off stimulation—the signal to noise ratio is clearly higher, especially at low spatial frequencies.

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